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BULLETIN
OF THE
TORREY BOTANICAL CLUB.

Vol. XIII.] New York, November, 1886. [No. 11.

The Pores of the Libriform Tissue.

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The objections against the imbibition theory of the passage of the sap through the cell walls, and the growing favor with which the opposite theory is regarded, namely: its passage through the cell lumina, have suggested a question in regard to some anatomical facts that have hitherto been disregarded. As the theory accounted for the upward movement of the water through the agency of the cell walls of the woody or libriform tissue of the stem, no special interest attached itself to the difference in the form or frequency of the pores of this tissue. Therefore, while the anatomy of the woody tissue has been thoroughly studied and described by various authors, Sanio, Hartig and others, certain points of difference in the libriform tissue have received no mention from these authors, and as these facts appear to have a direct bearing on the theory of water movement through the cell lumina, a brief consideration of them may not be wholly without interest.

A few words of explanation are here necessary to show why a difference in function is inferred from this difference in the anatomy of the pore. Assuming the passage of the sap through the lumina, it is plain that the different elements of the wood (holzkörper) contribute in different degrees to this result; other things being equal, those being most efficacious whose lumina have the greatest diameter. Therefore the tracheæ take the first rank and are supposed to be channels through which the water is passed upward to the leaves, instead of being mere reservoirs of water. Assuming this of the tracheæ, it may be supposed that the thin-walled tracheids have a similar function and rank next in importance, those at least whose walls are so thin that they are of little use as strengthening cells, and which differ from the real tracheæ only by the lack of direct communication with each other, and by their usually smaller diameter. It is well known that some of these tracheids are supplied with peculiar shaped pores whose function is generally conceded to be that of facilitating the passage of some part of the cell contents from one cell to another. Next we come to the tissue forming the subject of the present work, namely: the libriform or thick walled woody tissue. In many instances the cells of this tissue are found to possess pores of the same peculiar shape as those of the thin-walled tracheids. Hence a slight ground for the inference that these cells also serve to a certain extent as water carriers and rank next in importance to the tracheids, the passage of the water being facilitated by the same mechanical construction as in the cells of the latter class. Lastly we come to the remaining cells of the libriform tissue, which are supposed to be of the least importance in this respect, as they are supplied only with simple pores, such as are found in all parts of plant-organs wherever thick-walled cells occur, and where there is no reason for supposing any arrangement specially adapted to the rapid transport of water.

A second and perhaps better reason for this assumption, is the result of various experiments with the wood of coniferous trees, which contains no tracheæ nor thin walled tracheids, but with the exception of the cells of the medullary ray, consists entirely of thick walled tracheids abundantly supplied with these peculiar pores. The experiments of Robert Hartig and others have proved that no considerable amount of water passes through these cell walls, therefore furnishing strong presumptive evidence in favor of the assumption that the passage of water upward from one cell to another, in the case of the tracheids of the conifers, is in some way facilitated by these bordered* pores, which as before stated, correspond exactly in form with the bordered pores of the libriform tissue of dicotyledonous woods.

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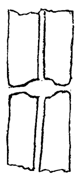
* The word bordered is used here in the sense of the German word behöft, and throughout this article the word border is used for the German word hof, when used with reference to the widening at the extremity of the pore next the outer surface of the cell wall.

Still another reason for supposing a functional difference between bordered and simple pores is founded on the fact, that whenever the libriform cells are used as reservoirs of starch, which is often the case, it has hitherto been found only in those with simple pores. In all the woods examined in the work described in the following pages only two exceptions to this statement were found, and these did not materially weaken the argument used.

An attempt has been made, as here described, to examine the wood of the principal dicotyledonous families, in reference to this characteristic of the libriform tissue and to show; first, to what extent it is possible for it to aid in the process of water-carrying, as shown by the presence or absence of these borders; second, how far this anatomical structure coincides with the morphological characteristics which are made the basis of the present system of classification and serve to determine the limits of genera, families, groups, etc.

It will be necessary at the outset to explain somewhat in detail what principle or definition has been followed in deciding to which class a pore belongs; for though in general, it is very easy to distinguish a bordered from a simple pore, many cases occur where the necessity for a clear and fixed definition is seen. In all thick-walled cells, where simple pores are found, there is, or may be, a tendency to a slight funnel-formed enlargement of the canal at the extremity where the two pores of the adjacent cells meet. The question is, what must be the form of this enlargement to give it the name border? As a test of this, examples were taken from the pores of bast and sclerenchyma cells, where there is no reason for supposing any adaptation to water transport. In many of these pores the canal widens sufficiently to present the appearance of a very small border. If we take, however, the so-called profile view, made either by a cross or longitudinal section through the border, and compare it with the same view of that of the pores of Coniferæ (see figures *a* and *b*) it will be seen that in the former the wall of the canal passes by a curve into this opening, while in the latter, it makes always a distinct angle. This was taken for a test, and in all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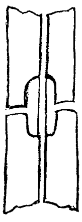
b

cases where a decided angle occurs, the pore is considered bordered (*behöft*). Sanio, in his work on the wood elements (Holzkörper), probably took another standard, as he has in several cases described pores as bordered, which, by this test, must be considered simple; for example—*Fraxinus*, *Betula* and others.

The principal genera of sixty-seven families were examined. Of this number there are only eight families in which the libriform tissue contains both bordered and simple pores, eighteen contain only bordered, and thirty-four only simple pores. The remaining seven families contain genera which do not agree in this respect. These present various points of interest in regard to the parallelism between anatomical and morphological characteristics, therefore they will be referred to more fully in the second part of the work.

If we begin with the most complex type, or that containing the greatest variety of elements, we find this illustrated by the eight families containing both kinds of pores in the libriform. Here we find not only the highest degree of differentiation of tissue, but also the greatest variety of means for water transport, according to the assumption that the greater amount of water is carried through the cell lumen. One example taken from this class will illustrate this and also the manner of arrangement of the tissues, in which is found a supposed adaptation to this function of the bordered pore. We omit here the part supposed to be played by the cells of the medullary ray and wood parenchyma, in the upward transport of water—not because it is less important, but on account of its lack of connection with the present subject; then we have, as before stated, the tracheæ, which take the first rank as water carriers, both on account of their size (diameter) and their open communication with each other; then the thin-walled tracheids, next the thick-walled or libriform cells with bordered pores, next the real libriform cells, or those containing only simple pores. The woody tissue of *Quercus* furnishes a typical illustration containing all these elements with great variation in size. If we make a cross-section extending through the growth of a single year—that is, giving us the picture of the so-called annual ring—we find the elements arranged in the following order :

SKETCH OF THE GROWTH FOR ONE YEAR.

f	CAMBIUM. Libriform, with bordered pores.	Autumn.
e	Libriform, with simple and bordered pores.	Summer.
d	Libriform, with only simple pores.	
c	Libriform, with simple and bordered pores.	
b	Tracheæ and tracheids.	Spring.
a	Spring wood, with only few libriform cells.	

The cells first formed from the cambium in the spring lie next to the inner limit of the annual ring (see *a*), and consist of large tracheæ and thin-walled tracheids with large bordered pores. Next follows zone *b*, in which the tracheæ and tracheids are much smaller in diameter, and the walls of the tracheids perceptibly thicker. In zone *c*, only a few tracheæ occur; the walls of the tracheids here are nearly as thick as in the real libriform cells, and contain bordered pores which diminish in size and frequency toward the middle of the year's ring or the summer's growth. Then follows the zone *d*, which consists almost entirely of thick-walled, simple-pored, libriform cells. This zone varies in size; in the sections examined it averaged between ¼ and ⅓ of the whole width of the year's ring. Then follows another zone, *e*, where the bordered pores again appear, of about the same size and frequency as in zone *c*. Lastly comes the autumn-wood, *f*, in which the pores are all bordered; they lie mostly on the tangential walls, but are not restricted to these; the borders are quite large, often reaching the size of those found in the thin-walled tracheids.

To explain the supposed adaptation here to the transfer of water at such times when the need is greatest, we refer once more to the coniferous woods, with which experiments have been made which verify some of the assumptions regarding the water transport, and furnish a kind of centre around which may be grouped other facts and conjectures. It is well known that the pores of the tracheids of the summer wood of the conifers lie on the radial walls, while those of the autumn wood are found almost exclusively on the tangential walls. It has been suggested that this arrangement is just what might be expected if these pores are designed to facilitate the passage of water. In the early spring, when the building process begins anew, there arises at the same time the necessity for a sufficient supply of water for the new cells, which necessity is met by these pores forming a direct communication with the cambium layer. This in case of the conifers is given only as a suggestion or conjecture; but whatever importance may be attached to it as such, may be applied with equal weight to the wood of *Quercus*, and also to that of the remaining genera of this and the other seven families. In these eight families where both bordered and simple-pored libriform tissue occurs, of which *Quercus* is given as the type, we find the last layers of the summer's growth, the so-called autumn-wood cells, contain bordered pores, nearly all of which are situated on the tangential walls, thus furnishing the same means for the rapid transport of water to the cambium layer in the spring as in case of the conifers. The first cells built in the spring are the large tracheæ and thin-walled tracheids, which arrangement appears also a part of the same plan, as the rapid growth occurring when the leaf-buds develop into leaves, must call for a large and rapid supply of water. Later in the season are built the strengthening cells, real libriform with simple pores, with no special provision for water transport; then in the fall again appear the pores with large borders.

In *Castanea* and *Fagus* the arrangement is the same as in *Quercus*, except that in *Fagus* the zone of simple-pored libriform tissue is very narrow. In the genera examined in Amygdaleæ, this zone is much wider than in any of the above mentioned cases, while in *Spiræa* the case is reversed, the greater part of the year's ring being made up of bordered-pored libriform. In the remaining families, Celastrineæ, Sapotaceæ, Campanulaceæ, and in *Buxus*, it is more difficult to determine the average amount of simple-pored libriform. In Celastrineæ and *Buxus* the greater part of the libriform tissue contains bordered pores. The family Myrtaceæ we have also included in this number, as it contains both kinds of libriform tissue in all the genera examined, with but one exception. In *Myrtus communis* no simple-pored libriform cells were found, though it is possible that they exist, but in such small quantities as to have escaped detection. In this family there is a marked difference in the quantity of the simple-pored libriform in the different genera, and it is difficult to give a very definite order of arrangement of the different layers. In general, it may be said, whenever the libriform of any part of the year's ring contains bordered pores, they are never wanting in the last layers of the year's growth, so that they stand in direct communication with the cambium layer in the early spring.

A few facts of interest in this connection may be mentioned in regard to the size of the border and position of the pores in the nineteen families where only bordered pores occur.

In the genera studied, all variations of size occur between the smallest and largest found. Among the smallest are those of *Erica* and *Tabernœmontana.* The length of the border in *Erica,* as seen in profile, is about 1½ micromillimeters, measured on the cross-section; the longitudinal section averaged a trifle longer, between 1½ and 2 mm. The largest were found in *Syringa, Drimys,* and a few others. One of *Drimys* was found to measure 9 mm., but this was an exception, as they average here from 6 to 7½. In *Syringa* they are between 6 and 7 mm. These larger ones compare very fairly with the size of the border in many of the Conifers. For example, those of *Pinus* and *Larix* measure from 7 to 7½ and 8 mm.

Frequently variations were found in genera of the same family, as in case of Ericaceæ, Magnoliaceæ and others, sometimes in the same specimen, as in *Quercus,* where they vary from 3½ to 5 mm., according to their position in the year's ring. One or two instances were found where the borders of the same cell differed in size.

Of all the genera examined in these eighteen families, *Erica* and *Tabernœmontana* are the most interesting, as they furnish the only exceptions thus far found, to the statement before made, that the simple-pored libriform cells are the only ones used as reservoirs for starch. Here the libriform cells contain very small starch grains and are furnished with bordered pores; the borders, however, are so extremely small, that in spite of their perfectly typical form, they can hardly be considered otherwise than as transitional between simple and bordered pores. The family Ericaceæ is also interesting on account of the difference in the size of borders found in its different genera. In *Erica* the border is exceedingly small, in *Calluna* not much larger, in *Ledum* and *Arbutus* a marked increase in size is seen, so in *Andromeda* and *Rhododendron* until at last in *Vaccinium* and *Oxycoccus* the border reaches a medium size; that of *Vaccinium*, in one instance, measuring 5 mm. Only in the genus *Erica* were starch grains present.

In the family Apocynaceæ there is also considerable variation both in the frequency of pores and size of borders, but in the latter case it is much less marked than in the family Ericaceæ. The borders of the genus *Tabernæmontana*, where the starch grains were found, are, if possible, even smaller than those of *Erica*, but perfectly typical in form.

In the majority of instances, the pores were situated on all sides of the cell. Exceptions to this occur in proximity to the limit of the year's ring. Here they are principally on the tangential walls. In a few families they show a decided preference to the tangential walls throughout. In *Drimys* the similarity between their arrangement and that of the pores of conifers is very noticeable. The specimen examined was a one year's stem; the pores are entirely limited to the radial walls, except in the last eight or ten layers next the cambium ring. Here they occur principally on the tangential walls. This genus resembles the conifers also in the size and frequency of the borders, and in the predominance of this tracheal element.

Of the thirty-three families containing only simple pores in the libriform tissue no special mention is necessary except as regards one point. Whatever may be the functional differences in the elements of the woody tissue, the extreme contrast between the most complex and simple forms suggests some plan for the division of labor in the more complex. If, as some authors have suggested, the office of the tracheæ is to supply the need of water in the leaves, caused by transpiration, while that of the tracheids is to supply the local demands, which exist in all living parts of the stem, it might be inferred, that in those cases where the libriform has only simple pores, there would be found thin-walled tracheids, and in cases where the libriform was liberally supplied with bordered pores, the other tracheal element would not be apt to occur in such large quantities.

(*To be continued.*)